

Heterochronic Processes in Human Evolution: An Ontogenetic Analysis of the Hominid Pelvis

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Australopithecus; *Pan*; *Gorilla*

ABSTRACT Changes in pelvic shape in human ontogeny and hominid phylogeny suggest that the heterochronic processes involved differ greatly from the neotenic process traditionally described in the evolution of the skull. The morphology of 150 juvenile and adult pelves of African apes, 60 juvenile and adult pelves of modern humans, two adult pelves and a juvenile hip bone of australopithecines (Sts 14, AL 288, MLD 7) was studied. Multivariate results, ontogenetic allometries, and growth curves confirm that the pelvic growth pattern in humans differs markedly from those of the African apes. The results permit the following conclusions. First, the appearance of a new feature (acetabulo-cristal buttress and cristal tubercle) at the time of human birth allows the addition of traits, such as the attainment of a proportionally narrower pelvis, with more sagittally positioned iliac blades. Pelvic proportions and orientation change progressively in early childhood as bipedalism is practiced. Other changes in pelvic proportions occur later with the adolescent growth spurt. Second, comparison of juvenile and adult australopithecines to modern humans indicates that 1) some pelvic traits of adult *Australopithecus* resemble those of neonate *Homo*; 2) the pelvic growth of *Australopithecus* was probably closer to that of apes, than to that of humans; and 3) prolonged growth in length of hindlimb and pelvis after sexual maturity seems to be a unique feature of *Homo*. The position of the acetabulo-cristal buttress and of the cristal tubercle on the ilium are similar in adult *Australopithecus* and neonate *Homo* suggesting that this feature may have been displaced later during hominid evolution. Progressive displacement of the acetabulo-cristal buttress on the ilium occurs both during hominid evolution (from *Australopithecus* to *Homo sapiens*) and human growth (from neonate to adult). This suggests peramorphic evolution of the pelvic morphology of hominids combining three processes of recapitulation (pre-displacement, acceleration and time hypermorphosis). The results lend credence to the hypothesis that no single heterochronic process accounts for all human evolutionary change; rather this reflects a combination of relative changes in growth rhythm and duration, including other perturbations, such as the appearance of new morphological features. *Am J Phys Anthropol* 105:441–459, 1998. © 1998 Wiley-Liss, Inc.

INTRODUCTION

In the past few decades, numerous studies have focused on the postcranial morphology of hominids and investigated their functional adaptation. The pelvic morphology of

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the first hominids involves peculiar static and dynamic conditions of bipedalism. The changes in pelvic and hindlimb proportions from *Australopithecus* to *Homo* now allow the latter to walk farther, with higher stride length and speed than the australopithecines (see, for example, Zihlman and Hunter, 1972; McHenry and Corruccini, 1978; Jungers, 1982, 1988, 1991; Jungers and Stern, 1983; Stern and Susman, 1983; Susman et al., 1984; Reynolds, 1987; Berge, 1994). From an evolutionary viewpoint, these morphological changes may be explained by two complementary approaches (Gould, 1977; Gould and Lewontin, 1979; Alberch, 1989, 1990; Maynard Smith et al., 1985; Devillers, 1989): First, there is an externalist approach, which refers predominantly to natural selection. Other factors affecting gene frequency in populations, such as gene flow, genetic drift and founder effect, are also aspects of an externalist approach. Second, there is an internalist approach, which refers to developmental constraints which induce genetic changes that may modify the bauplan of the body.

The role of developmental constraints in evolution is not easy to define. Alberch (1982, 1990) and Smith et al. (1985) suggest that they be defined as biases on the production of variant phenotypes or limitations on phenotypic variability. Thus, the internalist approach is not directly concerned with the question of adaptation, but rather limits the process of adaptation. For the present purpose, we notice, for example, that changes in pelvic ontogeny during hominid evolution seem to be related to changes in the adaptation of bipedalism from *Australopithecus* to *Homo*. Even though changes in the ontogenetic trend cannot be clearly explained by natural selection, changes in the evolutionary trend have a significance in terms of adaptation and may be controlled de facto by natural selection.

Neoteny in human evolution: evidence pro and con

Ontogenetic studies aim to elucidate morphology by analyzing how development produces changes in shape. Evolutionary changes in ontogeny involve the introduction of new features or temporal displace-

ment of existing ones, i.e., heterochronic changes (Gould, 1977; 1982; Alberch et al., 1979; Devillers, 1989; McKinney and McNamara, 1991). The notion of human evolution in terms of heterochrony is rooted in the fetalization theory of Bolk (1926), based upon the similarity of shape between the skulls of juvenile apes and adult humans. Numerous studies have pointed out that during ape ontogeny, the similarity disappears due to the strong facial growth (positive allometry) coupled with the weak cranial growth (negative allometry). In contrast, humans display an inverse development. Bolk and others assume that the human lineage displays a retarded development, retaining the juvenile features of ancestors.

To strengthen his theory, Bolk provided a list of other similarities observed in the whole body of adult humans and juvenile apes (cf. Gould, 1977). Most of these traits have now been rejected because they result from differences in adaptation rather than from different developmental processes. However, some of them were considered to be particularly convincing by Bolk and his contemporaries, and I shall return to their significance.

Many of these traits were considered by Schultz, whose work is of particular interest because he changed his position dramatically within his long career: he began as an ardent advocate of Bolk but later rejected his theory. Schultz (1923, 1926) used the recapitulation theory to argue that all the primates inherited a common ontogenetic sequence, which repeats phylogeny. He described this as a general trend with prosimians, monkeys, apes, and the various races of humans representing successive evolutionary steps. Schultz (1926) considered humans to be least specialized because they retained more primitive traits than do non-human primates. He selected certain arguments from his large range of anatomical data to strengthen the "stimulating theory of Bolk" (Schultz, 1927, p. 61), although he admitted that there are numerous anatomical traits that do not coincide with the fetalization theory but rather support its opposite (see also, Schultz, 1924, 1949). The 1950s saw a general change of opinion concerning human evolution in general, and

human races in particular; this forced Schultz to abandon some of his convictions. In a long chapter that summarized numerous morphological data on ontogenetic changes in apes and humans, Schultz (1956) accepted that the idea of a global retardation of man must be rejected. However, he estimated that in regard to skeletal, dental and postural development, chimpanzees grow more rapidly than humans who show a prolonged period of post-natal growth. He stated: "... the retention of fetal or infantile conditions, as is commonly claimed, has become an untenable theory with the advance in our knowledge of the ontogenetic processes in other primates" (1956, p. 959). In the same publication, he adopted a new position, which he maintained until his last scientific paper in 1973. Differences in rates of growth may produce comparatively retarded and accelerated growth processes in the various parts of the body (named "ontogenetic specializations") in man as well as in other primates. One could conclude that the neotenic theory seemed to have failed. The apparent neoteny of man is produced by differences in rates of growth rather than by a generalized retarded development (Schultz, 1973). Even his study of the human skull did not provide Schultz (1956) with arguments in defense of neoteny. For example, the ages at which the cranial sutures are obliterated do not support a retarded process of ossification. Contemporaries, such as Coupin (1928) and Vallois (1940), have also suggested that human body size and limb bone ossification are not retarded as compared with these processes in the great apes.

Nevertheless, until recently the theory of neoteny in human evolution has found much support. In other terms, it argues that our paedomorphic morphology results from a neotenic process, that combines a delayed maturation with an increased body size. Gould (1977) was among the first to assert that neoteny has played a key role in human evolution. For him, humans are "essentially" neotenous, and are characterized by a general retardation of development. His report continues: "this retardation established a matrix within which all trends in the evolution of human morphology must be as-

sessed" (p. 365). However, his convictions have been questioned largely because, like Bolk, Schultz and many others, Gould included in the neotenic process (*sensu stricto*), a retardation of ancestral rates of shape change, or paedomorphosis), prolongation in the time required for an apparent morphological shape retardation (peramorphosis). Shea (1989) later demonstrated that the increase in body size occurring with the prolongation of growth (time hypermorphosis) is incompatible with a paedomorphic process, which leads to dwarf individuals (time hypomorphosis) or individuals of the same size (rate hypomorphosis). Godfrey and Sutherland (1996) share this opinion about allometry. Thus, Shea (1989) rejected outright the hypothesis of a general neotenic process in human evolution. He also suggested that discovery of additional non-paedomorphic features could modify the theory.

McKinney and McNamara (1991) were yet more emphatic in their rejection of a role for neoteny in human evolution. They agree with the hypothesis of a peramorphic process which involves an overdeveloped brain by a prolonged growth during childhood and a retardation of maturity (hypermorphosis). However, they disagree with the hypothesis that there is a paedomorphic process which would preserve certain infantile traits. For example, in terms of flexion and growth of the base of the skull, adult apes retain more juvenile traits than do adult humans. Indeed, McKinney and McNamara (1991) propose that the apparent neoteny results from a delayed maturity and not a truly slow growth rate. On the other hand, it seems more probable that oversimplification may lead to additional errors of interpretation; this was suggested by Dean and Wood (1984) in a comparison of cranial growth curves in pongids and humans. In my opinion, the debate on neoteny is greatly confused by the belief that identical heterochronic processes occur in skulls and post-cranial skeletons, although we know that the growth of cranial and long bones differs in time, rhythm and velocity.

In contrast to information on the skull, there is very little information concerning heterochronic hypotheses on the post-cra-

nium. First, and as already mentioned, it is traditionally admitted that the delayed maturity of humans leads to an increased body size, or time hypermorphosis (Bogin, 1988; Leigh, 1996). The pelvis is a key element in the study of such heterochrony. Three bones compose the innominate (ilium, ischium, and pubis) and grow in length as do the limb bones and the overall stature do (Pineau, 1991; Berge, 1995a,b). Second, one may suppose that growth of the post-cranium involves other heterochronic processes. McKinney and McNamara (1991, mainly based on cranial data) suggested, in reference to Chaline et al. (1986), that "among numerous adaptations to bipedalism perhaps the most central is the pelvic restructuring which seems to result primarily from local accelerative process" (p. 316). However, such reports document the difficulty of approximating the ancestral pattern from which the human morphology has derived. In their study, McKinney and McNamara (1991) reported that pygmy chimpanzees are a good prototype for early australopithecine morphology. Indeed, the shape of the australopithecine skull shows some resemblance to that of chimpanzees. However, there is very little similarity regarding the post-cranium, and more specifically, the pelvic region. The skeletal and muscular systems of the first hominids present numerous specialized traits which are very distant from the pongid morphology. For example, the pelvic bones provide no proof that the very short human-like ilium, already characterizing the first hominids, derives from a very long chimpanzee-like ilium. Nevertheless Chaline et al. (1986) hypothesized this, and this morphological change is claimed to result from an accelerative process or an innovative trait.

Purpose of this study

In the present study I interpret the observed and measured pelvic morphological changes clearly both in hominid phylogeny and human ontogeny. Thus, morphological traits already present in the very early stages of human growth and hominid evolution are omitted, for instance the short ilium previously described. Also, the ancestral prototype is here considered to be an early

australopithecine already distant from the pongid-like prototype.

To define heterochronic processes in the pelvic morphology, I here consider four aspects: First, I compare the human and pongid patterns of growth in terms of allometry. Second, I compare the different stages of human growth in growth curves. Third, some aspects of pelvic growth in *Australopithecus africanus* are compared with juvenile and adult iliac morphology. Fourth, I compare human ontogeny (from neonate to adult) and hominid phylogeny (from *Australopithecus*, to *Homo sapiens*), thus evaluating heterochronic processes.

MATERIALS AND METHODS

The skeletal sample of modern specimens comprises: 26 pelves and 34 hip bones of juvenile and adult humans of known ages (coll. Orfila of the Institut d'Anatomie, centre Universitaire des Saints-Pères, Paris; and coll. of the Laboratoire d'Anthropologie, MNHN, Paris); 85 pelves of adult humans of unknown ages from various origins including 10 pelves of adult human pygmies (Laboratoire d'Anthropologie, MNHN, Paris; Laboratoire d'Anthropologie, Université Paris 7), and 150 pelves of adult and juvenile African great apes of unspecified ages. The ape sample comprises: 65 *Pan troglodytes* (Musée Royal de l'Afrique Centrale, Tervuren, Belgique, and Laboratoire d'Anatomie Comparée, MNHN, Paris); 28 *Pan paniscus* (Musée Royal de l'Afrique Centrale, Tervuren, Belgique); 46 *Gorilla gorilla* (Musée Royal de l'Afrique Centrale, Tervuren, and Laboratoire d'Anatomie Comparée, MNHN Paris).

The fossil casts comprise: the pelvis of an adult *Australopithecus africanus* Sts 14 (Robinson, 1972); the pelvis of an adult *A. afarensis* AL 288 (Schmid, 1983); and the ilium of a juvenile *A. africanus* MLD 7 (Dart, 1949a,b).

Eighteen dimensions of the pelvis and hip bones were measured (Fig. 1).

Bivariate methods. Ontogenetic allometry coefficients were calculated (Table 1) in humans and African apes by least-square regression of the pelvic dimensions against the pelvic length (log-data). The growth curves of four pelvic dimensions have also been compared in humans.

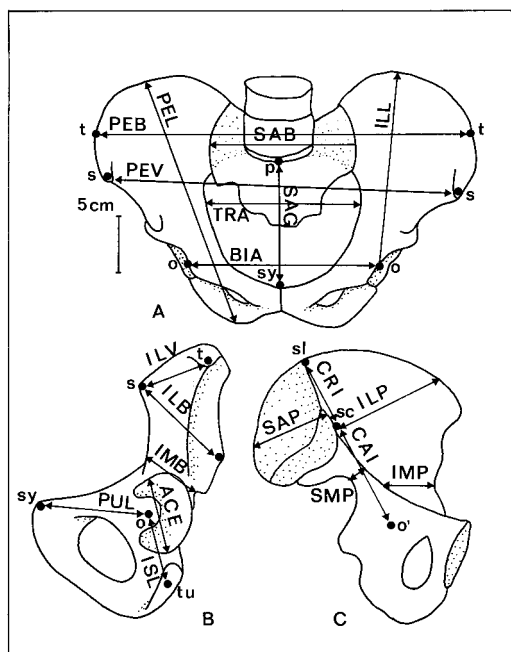


Fig. 1. Measurements of the human pelvis. **A:** Ventral view of the pelvis. **B:** External surface of the hip bone. **C:** Internal surface of the hip bone. Anatomical points used for measurements: o, center of the acetabular ring (o' on the internal surface of the hipbone); p, promontorium; s, anterior superior iliac spine; sc, scale-nion; sl, spina limitans; sy, symphysis; t, cristal tubercle; tu, tuberion.

Multivariate methods. The graphic results of two principal component analyses using double-centered and log-transformed data allow us first to compare the growth change in the pelvic patterns of humans and African apes, and second to position adult and juvenile Australopithecines in comparison to the extant species. The method, firstly defined by Mosiman and James (1979), was redefined later by Kazmierczak (1985), Berge and Kazmierczak (1986) from another mathematical viewpoint, closer to correspondence analysis, and renamed "logarithmic factorial analysis." This ratio approach allows elimination of the isometrical size of the individuals (see also, Jungers et al., 1995). This means that two geometrically similar individuals are projected onto the plane of the first two principal components with exactly the same coordinates. As is the case in the correspondence analysis, the variables corresponding to the shape data

are here projected onto the plane of the individuals to facilitate graphic interpretation. The cosine of the angle between two centered variables represents their correlation coefficient.

RESULTS

Pelvic pattern and pelvic growth in modern humans and African pongids

Previous studies have shown that the pelvic pattern of adult hominids is clearly distinct from that of the adult pongids (Jungers and Hartman, 1988; Berge, 1991a). Multivariate analysis allows us to describe interspecific and intraspecific (ontogenetic) variations within the groups (Fig. 2). Because the ages of the juvenile specimens are not specified, they are compared to adults as a group. However, Fig. 2 shows that human fetuses and human neonates are represented separately from older juveniles. The pongid material contains no fetal specimens. The first principal component (PC1: 90% of the total variance) clearly separates the hominid and pongid patterns. The projected variables on PC1 show the differences in terms of pelvic proportions. For example, the pelvis of the African apes is particularly long at the level of the iliac segments and on the ischium (CAI, ILL, SAG, PEL, ISL). The sacral region (SAB, SAP) is narrow, and the ilium is gracile at the level of the acetabulum (IMP, IMB).

Hominids as a whole share a common pelvic pattern which is characterized by opposite proportions, i.e., very short ilium and ischium, robust sacral region and robust ilium at the level of the hip joint. The second principal component (PC2: 4% of the total variance), on Fig. 2, corresponds rather to interspecific and ontogenetic variations. Interspecific variation was described earlier on the basis of a similar multivariate analysis using a large range of adult hominids and pongids including the orangs (Berge, 1991a). Ontogenetic variations in African apes coincide with the increased PC2 coordinates, whereas those of humans coincide with a decrease of PC2 coordinates from fetuses and neonates to older juveniles and adults.

PC2 coordinates of the variables indicate the following changes in pelvic shape: The

TABLE 1. Ontogenetic allometric coefficients calculated by least-square regression

Key	<i>Pan troglodytes</i>				<i>Pan paniscus</i>				<i>Gorilla gorilla</i>				<i>Homo sapiens</i>			
	N	b	sd(b)	R ²	N	b	sd(b)	R ²	N	b	sd(b)	R ²	N	b	sd(b)	R ²
PEB	63	1.09	0.03	0.95	26	1.11	0.03	0.98	44	1.06	0.02	0.99	17	0.99	0.02	0.99
BIA		1.26	0.05	0.92		1.20	0.07	0.92		1.18	0.03	0.97		0.85	0.03	0.98
TRA		1.29	0.05	0.92		1.29	0.07	0.93		1.17	0.03	0.97		1.01	0.02	0.99
SAB		0.92	0.04	0.90		0.95	0.06	0.91		0.84	0.04	0.91		1.24	0.03	0.99
SAG		0.95	0.03	0.95		0.90	0.05	0.93		0.96	0.03	0.95		0.90	0.03	0.98
PEV		1.09	0.03	0.95		1.11	0.03	0.98		1.06	0.02	0.99		0.91	0.02	0.99
ILB	63	1.16	0.04	0.94	26	1.16	0.04	0.97	44	1.06	0.02	0.98	52	0.98	0.01	0.99
ILL		1.01	0.02	0.98		0.98	0.01	1.00		0.99	0.01	1.00		0.97	0.01	0.97
PUL		1.10	0.04	0.93		1.10	0.04	0.97		1.05	0.02	0.98		0.97	0.02	0.97
ISL		0.99	0.03	0.96		1.08	0.03	0.98		0.96	0.02	0.98		1.05	0.02	0.99
CAI		0.99	0.03	0.95		0.90	0.05	0.94		0.99	0.03	0.97		0.88	0.02	0.97
CRI		1.03	0.04	0.93		1.05	0.06	0.92		0.89	0.04	0.90		0.99	0.02	0.97
ILP		1.17	0.03	0.95		1.27	0.03	0.98		1.19	0.03	0.98		0.97	0.02	0.99
SAP		0.93	0.06	0.82		0.94	0.08	0.85		0.79	0.04	0.90		1.05	0.02	0.98
IMB		1.00	0.05	0.86		1.04	0.06	0.91		1.01	0.04	0.95		0.90	0.01	0.99
ACE	30	0.84	0.06	0.85		0.75	0.05	0.90	11	0.65	0.05	0.93		1.09	0.03	0.97
ILV	0				0				0				50	1.27	0.04	0.94

Each pelvic dimension is regressed against the pelvic length (log-data). See, definition of the variables, Figure 1. N, number of specimens; b, allometric coefficients (regression slopes); sd(b), standard error of b; R², coefficient of determination.

growth pattern of African apes corresponds to a marked increase of the transverse pelvic dimensions, at the levels of the iliac blades (and especially of the iliac plane of the ilium), of the pelvic cavity. In contrast to that increase the transverse dimensions decrease proportionally at the level of the sacral region (sacrum and sacral plane of

the ilium). Humans display the opposite pattern of pelvic growth in that the transverse dimensions decrease at the levels of the iliac blades and of the pelvic cavity; conversely, the sacral dimensions show a relative increase. It bears mentioning that in the comparison of adult specimens (as in Berge, 1991a), the adult australopithecines

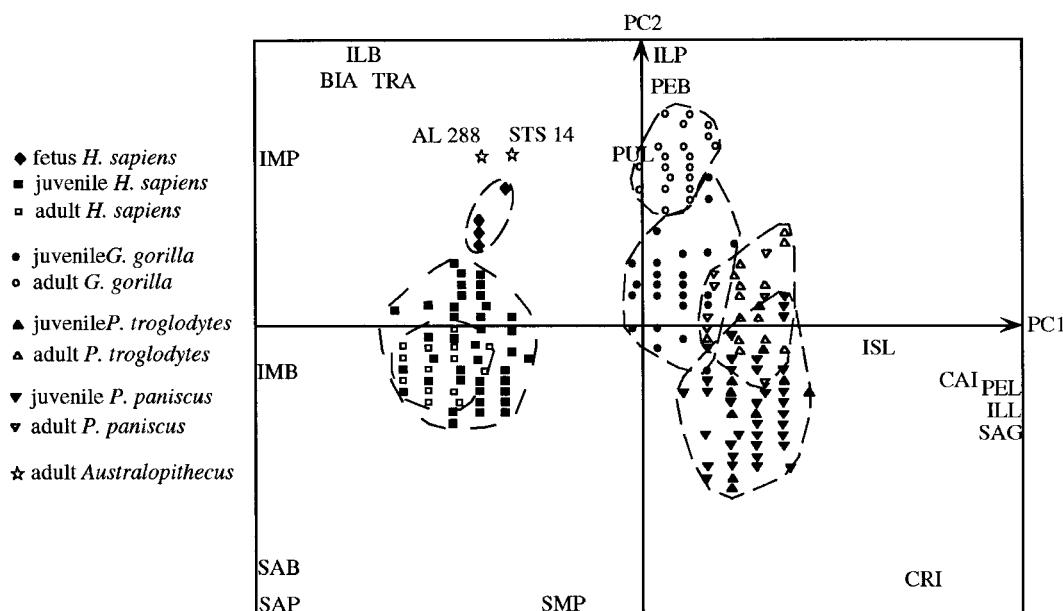


Fig. 2. Multivariate shape ratio analysis (covariance matrix of doubly centered data) of 17 pelvic dimensions among 202 juvenile and adult hominoids. Projection on the plane of the first two components (PC1, 90%, PC2, 4% of the variance, respectively). For key to variables, see Figure 1.

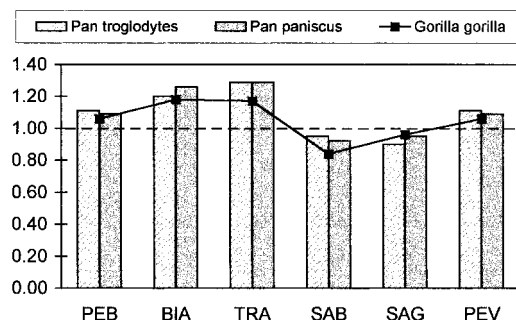


Fig. 3. The pelvic growth pattern of the African great apes defined by six ontogenetic allometric coefficients. On the X axis, allometric coefficients are calculated for the three species of African apes (for key to for measurements, see Figure 1; and calculation of the coefficients, Table 1). On the Y axis, the value 1 is the null hypothesis of geometric similarity (isometry), values greater than 1 are positive allometries, and values less than 1 are negative allometries.

(*Australopithecus africanus*, *A. afarensis*) lie relatively distant from adult humans on PC2, and closer to the position of adult gorillas. On the coordinates both of PC1 and PC2, adult australopithecines appear to be very much closer to fetal than to adult humans. The placement of the fossils is discussed below as part of the study of the ilium of the juvenile MLD 7.

The ontogenetic allometric coefficients of each species more clearly define the ontogenetic patterns (Table 1). Figures 3, 5 and 6 visualize these allometric variations by means of histograms. In Figure 3, the three species of African apes display approxi-

mately the same pattern of pelvic growth. Their relative growth changes correspond to a strong increase of the pelvic breadth at the level of the iliac blades, as well as at the level of the pelvic cavity (positive allometry); the breadth of the sacrum also decreases proportionally (negative allometry). Also, the breadth of the ape ilium increases considerably at the level of the iliac plane, whereas it decreases proportionally at the level of the sacral plane. This change is also noted in Figure 4 by comparing a 2-year-old chimpanzee with older specimens. For example, the pelvic breadth at the levels of the iliac blades and of the pelvic cavity. In contrast, the sacrum does not increase in breadth and consequently it becomes proportionally narrower, as does the acetabular ring. Figures 5 and 6 illustrate the change in human pelvic proportions in comparison to those of chimpanzees (*Pan troglodytes*). Fig. 5 shows that size-related shape changes in humans lead to fully different patterns of pelvic growth, characterized by increased transverse dimensions of the sacral region (positive allometry), and above all by a relative decrease of the pelvic breadths at the levels of the iliac blades and of the pelvic cavity (negative allometry). Some pelvic dimensions grow less than others. For example, Fig. 5 shows that the anterior pelvic breadth (PEV) becomes proportionally lower in humans (negative allometry), whereas the maximal pelvic breadth (PEB) scales isometrically. Another example is that the biacetabular diameter

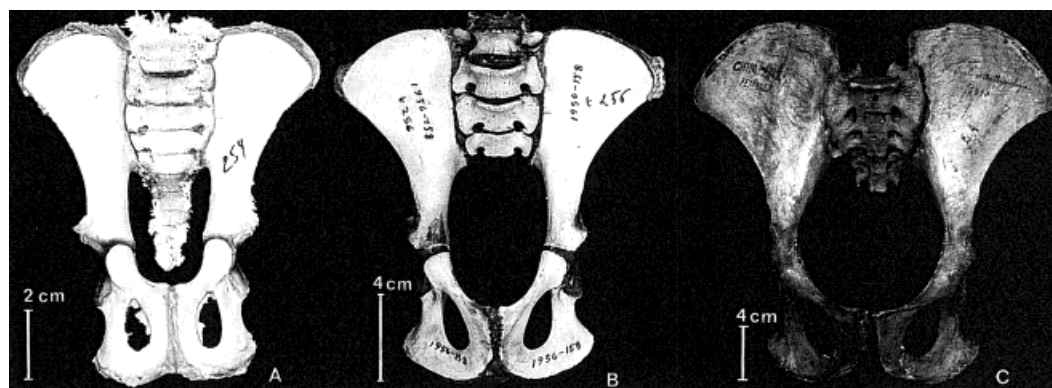


Fig. 4. Three different stages in the pelvic growth of *Pan troglodytes*. Left, juvenile approximately 2 years old; middle, older juvenile of unspecified age; right, adult.

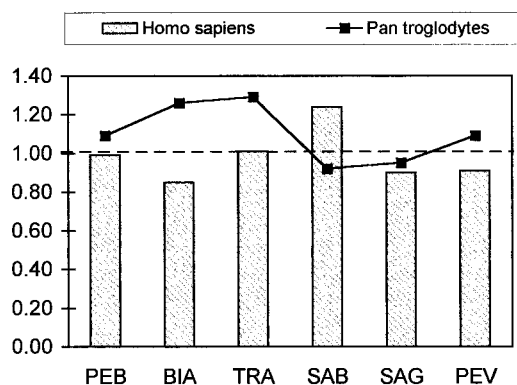


Fig. 5. The pelvic growth pattern in modern humans as compared to that of the common chimpanzee. On the X axis, allometric coefficients are calculated for the two species (for explanation, see Figure 3).

(BIA) scales negatively in humans, whereas the transverse diameter of the pelvic inlet (TRA) scales isometrically. Fig. 6 also shows that in humans the caudal segment of the ilium (CAI) increases negatively, the cranial segment (CRI) isometrically, and the ischium segment (ISL) positively. Also, the acetabulum (ACE) grows differently in humans (positive allometry) than in chimpanzees (negative allometry).

These morphological results permit several observations. First, multivariate analysis indicates clearly that most of the pelvic traits that define the outlines of the pelvic pattern in humans are already present in fetuses and neonates. For example, the very short ilium at the level of the caudal segment, and the proportions of the sacral plane of the ilium, separate humans as a group from the rest of the primates. Also there is very little resemblance between human fetuses and African apes. Secondly, the allometric components indicate that the pelvic growth patterns clearly separate modern humans from African apes. The main difference in the pelvic growth of apes and humans concerns the iliac blade the breadth of which increases more than its length in the former and the contrary in the latter. One of the consequences is that the breadth of the pelvis does not increase in humans during growth, as it does in other species. This peculiar trait will be shown to result from an important change in the shape of the human iliac blade during growth.

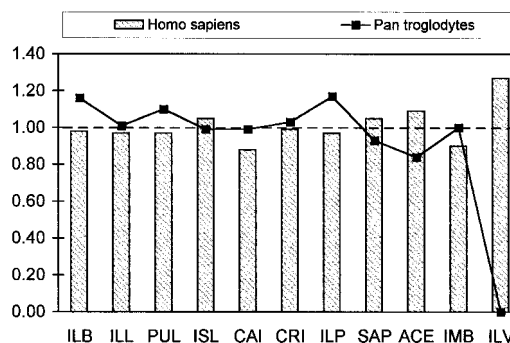


Fig. 6. The hip bone growth pattern in modern humans as compared to that of the common chimpanzee. On the X axis, allometric coefficients are calculated for the two species (for explanation, see Figure 3).

The different stages in the pelvic development of humans

The shape of the human pelvis starts to change at the beginning of the life rather only during childhood. Fig. 7 provides evidence for the following observations: First, most traits that characterize the human pelvis already occur in the fetal pelvis. For example, prior to the time of birth (term), the sciatic notch and the auricular surface have already obtained their characteristic shapes. Moreover, the surprisingly short caudal segment of the ilium (the segment CAI), which links the sacrum to the hip joint, is already very short and consequently characteristic of the human condition. In contrast, the human fetus has a flat and laterally positioned ilium as a sole "ape-like" trait. At this early stage, the site of maximal pelvic breadth (PEB) lies between the anterior superior iliac spines as it does in non-human primates; it is therefore superimposed on the anterior pelvic breadth (PEV). Second, by the time of birth, the iliac blade has become oblique and slightly curved. This shape change leads to the formation of the acetabulo-cristal buttress, a new trait which appears on the external face of the ilium and ends on the iliac crest by the cristal tubercle (see Fig. 8). However, at birth, PEB is very close to PEV because the acetabulo-cristal buttress is still very close to the anterior border of the ilium (and the iliac tubercle is close to the anterior superior iliac spine). Third, it is only later, here seen

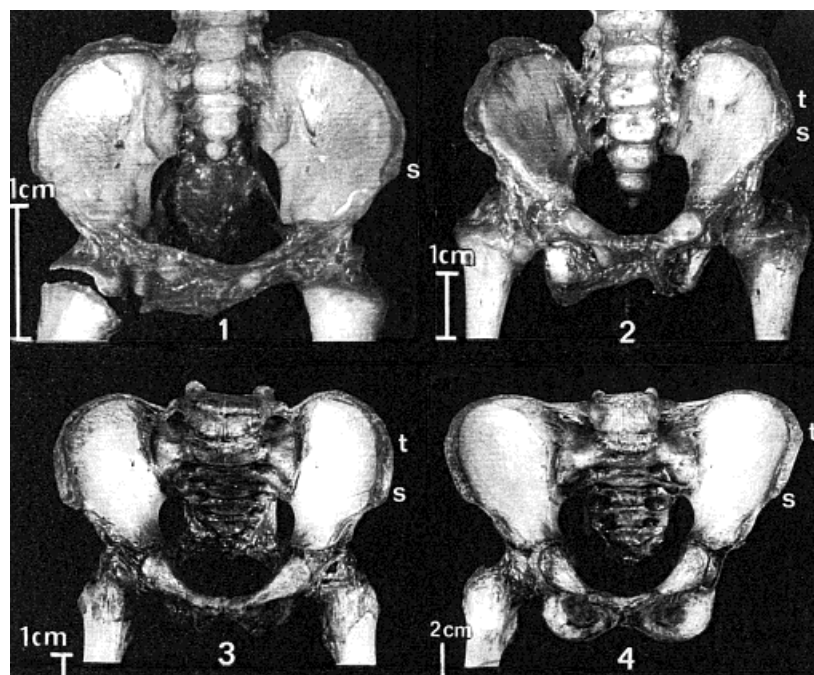


Fig. 7. Four different stages of pelvic growth in *Homo sapiens*. 1: Fetus of 5.5 months (PEL: 2.0 cm). 2: Neonate (PEL: 4.2 cm). 3: Child of 2 to 3 years of age (PEL: 10.3 cm). 4: Child of 10 years of age (PEL: 14.4 cm). s, anterior superior iliac spine; t, cristal tubercle.

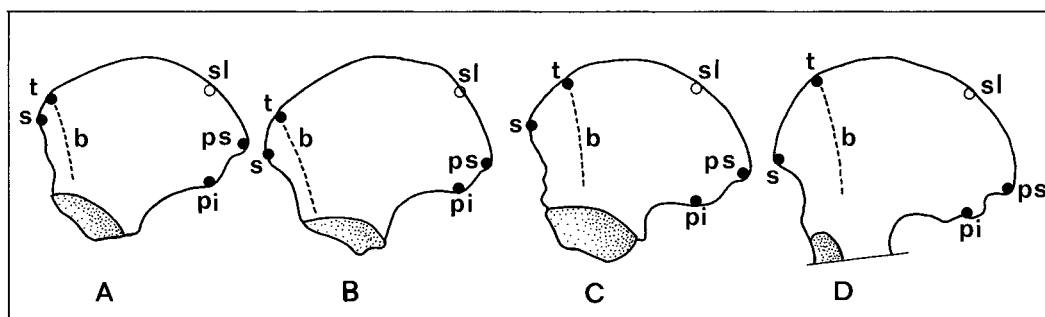


Fig. 8. The change in the shape of the ilium in human ontogeny (external face of juvenile and adult ilia). A: Neonate (ilium length: 3.3 cm). B: Juvenile aged 1 year, 7 months and 24 days (ilium length: 5.2 cm). C: Juvenile aged 10 years (ilium length: 9.6 cm). D: Adult (female pygmy; ilium length: 11.3 cm). A, B, C, without iliac crest. b, acetabulo-cristal buttress; pi, posterior

inferior iliac spine; ps, posterior superior iliac spine; s, anterior superior iliac spine; sl, *spina limitans* (sl is situated on the internal face of the ilium; see Figure 1); t, cristal tubercle. The two points sl and pi are arbitrarily placed on a vertical axis. Note the relative increase of the distance s-t during growth (see text).

in the pelvis of a 2-year-old child, that the shape and orientation of the ilium then is more curved ventrally and an internal iliac fossa forms. PEB is now clearly displaced into a more backward position whereas PEV has moved forward. Fourth, in the pelvis of a

10-year-old child, the incurved shape of the iliac blade is accentuated, and the distance between PEB and PEV increased.

The change in human pelvic shape during ontogeny has its roots in the change in the shape of the ilium. Fig. 8 illustrates the

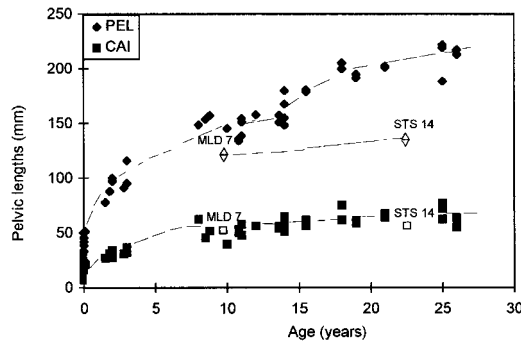


Fig. 9. Growth curves of two pelvic lengths in modern humans and australopithecines. X axis: age in years (0: birth). Y axis: PEL and CAI (see Figure 1). MLD 7, juvenile australopithecine aged less than 10 years (see text); STS 14, adult australopithecine.

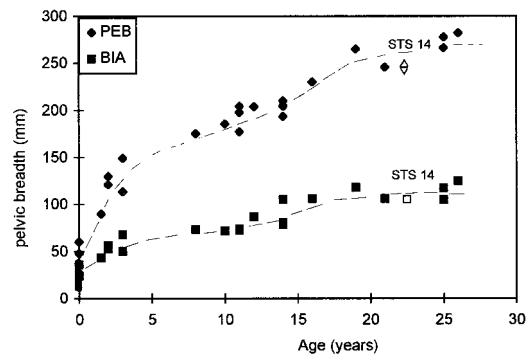


Fig. 10. Growth curves of two pelvic breadths in modern humans and australopithecines. X axis: age in years (0: birth). Y axis: PEB and BIA (see Fig. 1). MLD 7, juvenile australopithecine aged less than 10 years (see text); STS 14, adult australopithecine.

“displacement during growth” of the acetabulo-cristal buttress and the cristal tubercle on the external face of the human ilium. At the time of birth the buttress appears as a small thickening in the iliac wall, visible on the external face of the ilium. However, the cristal tubercle is hardly visible at this early ontogenetic stage, it being very close to the anterior superior iliac spine. The buttress, also hardly visible, lies close to the anterior border of the ilium. After birth, the size and shape change and the acetabulo-cristal buttress and the cristal tubercle appear to have been displaced to a more backward position, with the opposite displacement of the anterior superior iliac spine. Also, the ilium becomes more incurved, and more enlarged dorsally.

We may now use growth curves to determine changes in the shape of the ilium and pelvis during ontogeny. Growth curves aim to specify different stages and to monitor variations in rate, rhythm and velocity of growth. Four growth curves are here used to compare variations for the pelvic length and breadth (Figs. 9, 10). In both cases, some pelvic dimensions almost stop growth before the period of puberty or grow only slowly thereafter, other dimensions in contrast continue to grow significantly. For example, Fig. 9 shows that the caudal portion of the ilium (CAI) attains almost its adult length by puberty (which on the graph corresponds to a plateau lying approximately between 10 to 15 years of age). In contrast, the total length of the pelvis (PEL) continues to grow mark-

edly and only attains its adult size later (at around 16 years for females and 21 for males). Also, the biacetabular diameter (BIA) increases very slowly after the age of puberty, whereas the maximal pelvic breadth (PEB) continues to increase after puberty (Fig. 10). In other terms, the prolongation of the adolescent period corresponds to a noticeable increase in pelvic length and breadth. However, this increase in pelvic size is not followed by an increase for all the pelvic segments. Thus, the interarticular segments (CAI, BIA) cease growth prior to or during puberty.

Some aspects of pelvic growth in *Australopithecus africanus*

Dart (1949a,b) was the first to describe the left ilium MLD 7, and a portion of the right ischium MLD 8 found in the same breccia; he suggested that these pelvic bones come from the same individual as the adolescent mandible MLD 2 found nearby (Dart, 1948). After comparing the bones with those of a child of approximately the same stage of growth, he concluded that the mandible came from an australopithecine of 12 years of age and the pelvic bones from a subject of around the same age (Dart, 1948, 1949a,b). Another left ilium (MLD 25 found later) is illustrated in Dart (1958) and compared with MLD 7. MLD 25 and MLD 7 have similar ages and similar proportions. MLD 25, which is not included in the morphometric study, is discussed later on the basis of tracings given in Dart (1958).

Given that there is no proof that the pelvic bones MLD 7 and MLD 8 belong to the same individual as the mandible MLD 2, the juvenile ilium is considered on the basis of the pelvic bones alone. The ilium is clearly separated from the ischium and pubis, the acetabulum is not ossified, and the iliac crest is not fused to the iliac blade. Whether or not it belongs to the same individual, the ischium is not completely ossified at the level of the ischial tuberosity and at the level of the acetabulum. Curgy (1965) recorded the degree of ossification of the pelvic bones in apes and man. His work suggests that if MLD 7 follows the human growth pattern it might be considered to belong to a juvenile, less than 13 years of age. If MLD 7 follows the growth pattern of a common chimpanzee, it would be less than 10 years old. A chimpanzee-like growth and an age of less than 10 years (i.e., 8 or 9 years of age) is also more likely in the light of the following results.

Comparison with the adult pelvis Sts 14, allows several observations on MLD 7. The length of the ilium is similar in juvenile and adult specimens (Fig. 11). This is never true for modern humans within comparisons among individuals younger than 10 years of age and adults from the same population (Berge, 1995a, and Fig. 9). Fig. 9 shows that the growth spurt of the pelvic length after puberty is particularly marked in humans; in contrast it seems to be limited in australopithecines, witness the comparison of the juvenile MLD 7 (the pelvic length is estimated from the iliac and ischial lengths) to the adult Sts 14. As far as the comparison is representative for the australopithecine population, this could indicate that they ceased to grow in pelvic length at around 8 or 9 years of age. Other pelvic data seem to confirm a short period of growth. The longitudinal ilium proportions (CAI, PEL) seen in Fig. 9 are similar for juvenile and adult australopithecines, as well as for juvenile humans. On the contrary, they differ in adult humans because PEL increases at the end of the adolescent period by which time CAI has already ceased growth. Thus, the iliac morphology of MLD 7 suggests that *Australopithecus* lacks the growth spurt in pelvic length at the end of the adolescent period.

On the other hand, in *Australopithecines* the juvenile ilium MLD 7 has transverse proportions differing markedly from those of the adult (Fig. 11): the breadth of the iliac plane (ILP) scales from the juvenile to the adult (the damaged portion on the right ilium of Sts 14 was completed symmetrically from the left ilium), whereas the sacral plane (SAP) maintains the same proportions. This growth change in iliac shape is clearly visible of the multivariate analysis (Fig. 12). The adult australopithecines, which lie very far from adult humans, are very close to human fetuses and neonates. In contrast, the juvenile ilium MLD 7 seems to be more "human-like" because it lies closer to modern humans of its age. The morphological change, from MLD 7 to Sts 14 and AL 288, corresponds to an increase of PC2 coordinates, as previously described in growth of African ape (see Fig. 2). This result suggests that the pelvic growth pattern in australopithecines fully differs from that of modern humans, being closer to that of African apes not only in terms of growth duration but also in terms of shape change. In Fig. 12, the divergent growth trajectories observed in humans and australopithecines increase morphological differences between adult *Australopithecus* and adult *Homo*.

Parallel change in pelvic shape between human ontogeny and hominid phylogeny

A previous study has demonstrated that the ilia of an adult australopithecine and a neonate human have a very similar shape (Berge, 1996). Multivariate analyses disclose that the adult *Australopithecus* and the human fetus have similar pelvic proportions (Figs. 2 and 12). The australopithecine pelvis resembles that of a neonate in its iliac morphology: both are characterized by the ventral situation of the cristal tubercle close to the anterior superior iliac spine, and by the acetabulo-cristal buttress close to the anterior border of the ilium (Figs. 8 and 13). Such iliac morphology is also described as being shared by *Australopithecus africanus*, *A. afarensis* and *A. robustus* (Dart, 1958; Zihlman, 1971; Zihlman and Hunter, 1972; Lovejoy et al., 1973; Lovejoy, 1975), whereas the iliac morphology of *Homo erectus* is closer to that of modern humans (Sigmon, 1986). We observe here a "progressive"

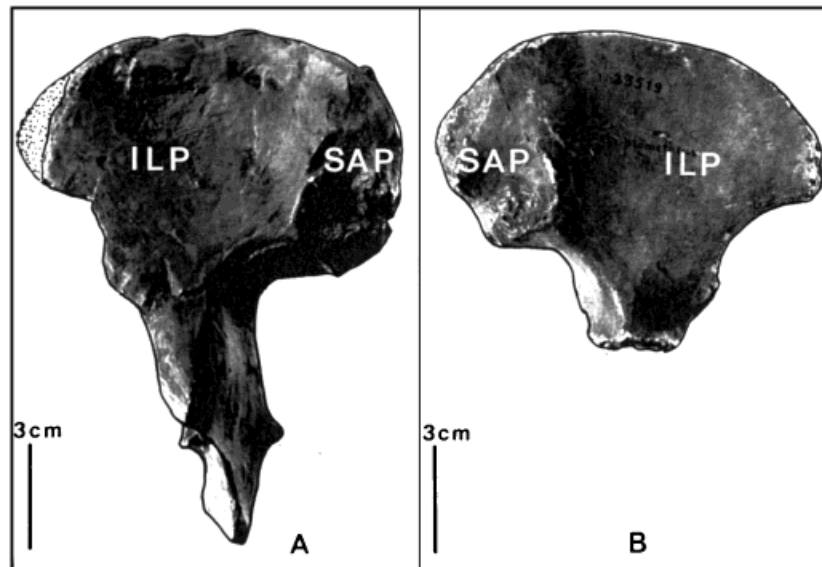


Fig. 11. The juvenile ilium MLD 7 (B) as compared to the adult hip bone Sts 14 (A). Internal view of the ilia with the same scale. ILP, iliac plane; SAP, sacral plane.

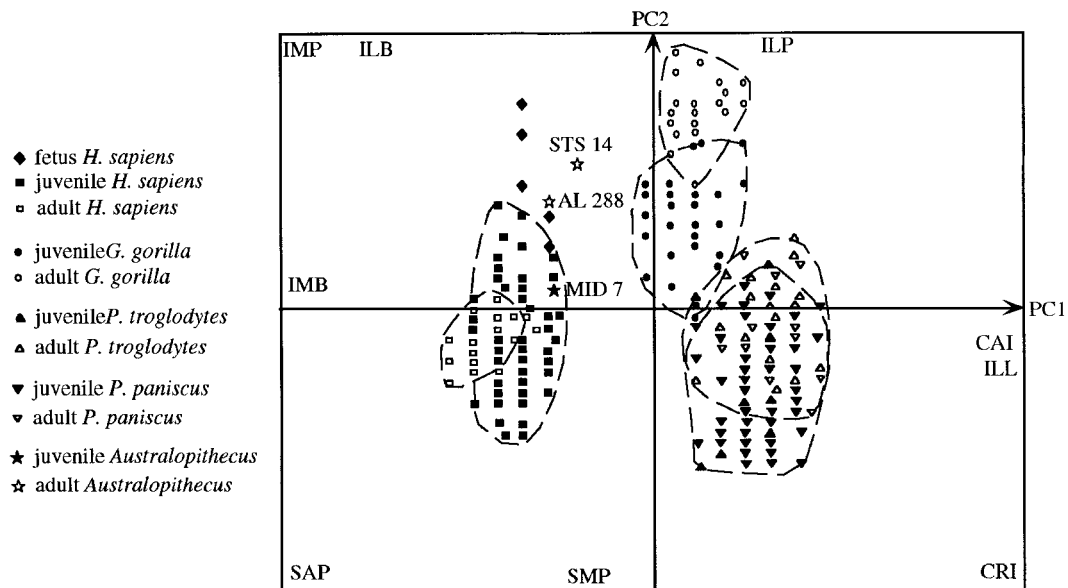


Fig. 12. Multivariate shape ratio analysis (covariance matrix of doubly centered data) of nine ilium dimensions among 218 juvenile and adult hominoids. Projection on the plane of the first two components (PC1, 85%, and PC2, 9% of the variance, respectively). For key to variables, see Figure 1.

change in iliac shape in hominid evolution, from *Australopithecus* to *Homo erectus*, and *H. sapiens*. The acetabulo-cristal buttress appears to be “progressively displaced” further from the anterior border of the ilium,

and the cristal tubercle further to the anterior superior iliac spine. The displacement of the iliac buttress on the external surface of the ilium, resulting from the double movement (cristal tubercle and anterior superior

iliac spine), leads to a modification of the overhall iliac shape. As in human growth, from neonate to adult, the iliac blades become more sagittally positioned in hominid evolution, with increased curvature of the anterior part of the ilium.

DISCUSSION

General data

The list of morphological traits given by Bolk (1926) to strengthen the neotenic theory is quoted by Gould (1977) as particularly vague and confusing. Some of these traits concern the post-cranium, for example: "the structure of the hand and foot; the form of the pelvis; the ventrally directed position of the sexual canal in women" (Gould, 1977, p. 357). Schultz (1926, 1927) also considered the overall development of body proportions to be retarded in humans as compared to those of modern apes. However, later, he interpreted some of these body proportions, such as those of the limb and foot, and the lumbo-sacral promontory, as resulting from an accelerated development (Schultz, 1949). In my opinion, interpretation of such traits in terms of acceleration or retardation is irrelevant because it assumes that all primates share a common ontogenetic condition within a common phylogenetic trend. Schultz (1949) described ontogenetic changes in a trend arising from the "primitive condition in lower primates" (monkeys) that leads to the "simian condition nearest Man" (apes), and then to "average condition in Man" (p. 213-214). For example, the lumbo-sacral promontory is described as being absent in monkeys, remaining moderate in apes, and becoming very pronounced in humans (i.e., an accelerated process). However, the angular values on the vertebral column of primates measured by Schultz (1961) indicate that the lumbo-sacral promontory corresponds to functional adaptations which differentiate humans, and to a lesser extent baboons, from the other primates. In the same way, the ventrally opened pelvic cavity above referred to as a neotenic trait in women is also shared by men, and corresponds to specific visceral and obstetrical conditions of hominids (Berge et al., 1984).

Thus, other arguments have to be found to support heterochronic hypotheses. The main

difficulty concerns the choice of a valuable ancestral prototype for hominids. The pelvic morphology of African apes is too different from that of the first hominids to represent a good ancestral pattern (Figs. 2, 12). We may also argue that African apes and modern humans do not share a single growth pattern for allometric changes of the pelvic morphology (Figs. 3, 5). Thus, the pelvic rests of early hominids are a very useful source of information. One may object that an ontogenetic hypothesis should not be founded on a few specimens. However, I would propose two main arguments to strengthen such a reconstruction. The first argument is the change in iliac shape observed from the juvenile MLD 7 to the adult australopithecines (i.e. increase in iliac breadth at the level of the iliac plane) which resembles ontogenetic changes observed in African apes (Fig. 12). This suggests that the pelvic growth pattern in early hominids may correspond to the generalized growth pattern in Hominoidea. On the contrary, as discussed below, the human pattern in iliac growth derives from new anatomical features leading to a complete change in pelvic shape. The second argument is the similarity in iliac size and shape in the juvenile MLD 7 and MLD 25 studied by Dart (1958). As is the case in apes, adolescent australopithecines show a noticeable change in ilium breadth. In short, the African apes should not be used as a prototype for ancestral pelvic morphology, but they can be used as a prototype for the ancestral pelvic growth pattern in terms of shape change and growth duration (see, below).

Comparison of the direction of growth of the pelvic bones in humans and common chimpanzees led Barham (1971) and Coleman (1971) to the conclusion that the pelvic regions are more affected by the magnitude and velocity of growth than by changes in its directions. Differences in magnitude of growth are expressed here by ontogenetic allometries (Figs. 3 and 5). The results indicate that the three species of African apes share a common pattern of pelvic growth, despite morphological differences already present in the youngest chimpanzees and gorillas studied (see Fig. 2). One of the most remarkable trait of their pelves is that it

becomes very broad at the level of the iliac blades.

Schultz (1930) and many of his contemporaries, such as Straus (1929), Waterman (1930) and Reynolds (1931), believed that the increase of the iliac breadth is a perfect example of the recapitulation theory. Schultz (1930) described a similar increase in width of the ilium in ontogeny (in African apes and humans) and in phylogeny (from monkeys, to apes and humans). In the present study, multivariate methods and allometric coefficients indicate clearly that the human growth leads to a relative decrease of the ilium breadth at the level of the iliac plane (internal iliac fossa). During growth, the iliac blade becomes more incurved and more sagittally positioned, with the relative displacement of the acetabulo-cristal buttress in a more dorsal situation (Fig. 8). Consequently, the human pelvis becomes proportionally narrower with growth, not only between the anterior superior iliac spines but also between the hip joints (Fig. 7).

The acetabulo-cristal buttress is a key-element in understanding the evolution and growth of the human pelvis. The acetabulo-cristal buttress, which is here described as a thickness ending on the iliac crest by a tubercle, is a uniquely hominid feature which appears at the time of birth in modern humans. The consequence of this new feature is an important change in the pelvic growth pattern. A comparison between modern humans and African pongids indicates that non-human primates and other mammals never have an acetabulo-cristal buttress; however, some large-bodied animals, such as gorillas, may support their visceral mass with broad and incurved iliac blades (pers. observation). This trait which differentiates humans from apes and monkeys was mentioned by Mednick (1955), but not by Straus (1929) and Schultz (1930), who placed humans close to gorillas on the basis of their pelvic morphology.

A different buttress pattern occurs in early hominids. Most of the authors consider that the cristal buttress in australopithecines is homologous to that of modern humans even though it lies in a distinct position (Mednick, 1955; Zihlman, 1971; Zihlman and Hunter, 1972; Lovejoy et al., 1973; Lovejoy, 1975;

Sigmon, 1986). However, Sigmon (1986) gave the two buttresses different names. Her acetabulo-spinous buttress of *Australopithecus* lies ventrally and her acetabulo-cristal buttress of *Homo* lies dorsally (the case of SK3155 described by Sigmon as having a human-like buttress has to be reconsidered; Berge, 1993). The present study suggests that all hominids share a common acetabulo-cristal buttress. This has changed progressively both in human ontogeny and hominid phylogeny (Figs. 8, 13). Moreover, a previous paper has demonstrated the great similarity in iliac shape between adult *Australopithecus* and neonate *Homo* (Berge, 1996). However, the australopithecine buttress is hardly visible on the adolescent ilium MLD 7 (Dart, 1949a). This suggests that their buttress pattern was formed later ontogenetically than in modern humans, probably during childhood or during adolescence. Thus, the buttress pattern arising at the end of the growth had no significant influence on the growth of the ilium which retains ape-like shape changes (increased PC2 coordinates from MLD 7 to Sts 14 in Fig. 12).

Recent studies on the dental development suggest that the growth duration in early hominids was more similar to that of apes than of humans (Bromage and Dean, 1985; Smith, 1986; Bromage, 1987; Smith et al., 1995). Smith et al. (1995) suggested that delayed maturation began in early *Homo* and reflects the extent of its brain expansion. For Bromage (1987), the delayed maturation is not only a cranio-dental process but also one for the whole body. He estimates that the increase in body size from *Australopithecus* to *Homo* results directly from a global retardation of growth. However, cranial and post-cranial bones do not grow for the same period, and consequently it is necessary to consider them separately. In Bogin (1988), for example, growth curves indicate that modern humans attain adult head size at 12 years of age, whereas they attain adult stature near age 16 in females and 18 in males. The period of puberty, which corresponds to a noticeable spurt of the body length (hindlimb length plus stature), is generally described as a feature uniquely human (Bogin, 1988). This is not the case for the body mass, its growth com-

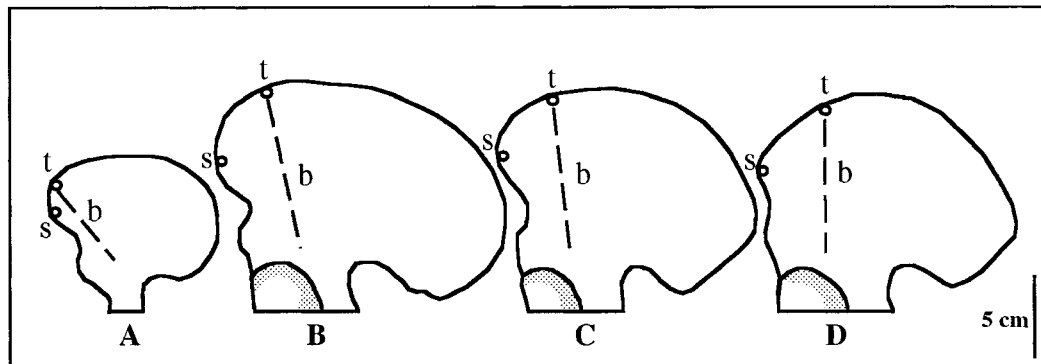


Fig. 13. The change in ilium shape in hominid phylogeny. External face of adult left ilia. **A:** *Australopithecus africanus* (Sts 14). **B:** *Homo erectus* (Tautavel). **C:** *H. neandertalensis* (Düsseldorf). **D:** *H. sapiens*. Same scale. s, anterior superior iliac spine; t, cristae tubercle; b, acetabulo-cristal buttress. Adapted from designs taken from Endo and Baba (1982).

monly shows a spurt in human and non-human primates (Leigh, 1992; Leigh and Shea, 1996).

The study of iliac growth is of particular interest because the longitudinal growth is similar to that of the length of a long bone, whereas its growth in width is as the breadth of the trunk. Thus, changes in ilium length and changed proportions from the juvenile MLD 7 to adults Sts 14 and AL 288 reveal important data concerning the growth pattern of australopithecines. We observe first that the ilium of an adolescent, which is estimated as being around 8 or 9 years old, in comparison to African apes, had already attained its adult size in terms of ilium and hindlimb lengths and consequently in terms of stature. On the other hand, the growth of australopithecine was probably marked by a noticeable spurt of transversal dimensions of the trunk and body mass at the end of the adolescence. Indeed, in the ilium of adults, we can see that the breadth of the iliac plane has increased considerably since the juvenile stage. This is the reason why the adolescent ilium MLD 7 appears to be more "human-like" than is that of adults (Fig. 12).

I propose that a connection between body proportions in adult australopithecines and the hypothesis of an ape-like growth pattern may be established. The very short stature and short hindlimbs have to be connected with the limited growth of long bone length at the end of the adolescence. In the same

way, the very broad pelvis and the funnel-shaped thorax may also indicate that transverse growth of early hominids was similar to that of apes and showed a significant increase in body weight at the end of the adolescence.

Evolutionary interpretation in terms of functional adaptation

In modern humans, the acetabulo-cristal buttress and the iliac tubercle appear at birth. In terms of functional adaptation, the acetabulo-cristal buttress marked the start of the deflection of the iliac blade in the anterior region. The thickening of the bone at this level is generally interpreted as a structural pattern corresponding either to the compressive forces occurring in bipedalism, or to the line of action of abductor muscles which laterally balance the pelvis (see, for example, Mednick, 1955; Zihlman, 1971; Lovejoy et al., 1973; Arsuaga, 1981; Stern and Susman, 1983). It is important to note that the iliac tubercle appears very early in human ontogeny. This suggests that the acetabulo-cristal buttress and the iliac tubercle are probably genetically determined. However, other pelvic features, such as the curvature of the iliac blade, or hindlimb features, such as the oblique position of the femoral diaphysis (Tardieu and Trinkaus, 1994), are influenced directly by gravitational effects, and are probably determined less directly.

Thus, it is only later, at around 2 years of age, when children begin to stand up and walk, that the orientation of the ilium changes and it becomes more incurved. A fully shaped ilium is attained in children at about 8 years of age (Berge, 1995a,b). For example, we may note that the interarticular segments CAI and BIA, which are particularly stressed in bipedalism, cease to grow at this age; in contrast, other segments related to pelvic size continue to grow after puberty (Figs. 9, 10). It is also in early childhood, at around the age of 6 years, that the ability to control lateral balance and to coordinate body segments in walking, is fully attained (Assaiante and Amblard, 1995). Thus, the pelvic growth occurring after 6 or 8 years of age does not fundamentally modify the main functional parameters. However, the growth spurt in hindlimb length at the end of the adolescent period increases both stride length and speed, and consequently facilitates running (Alexander, 1984).

It is most probable that the acetabulocrystal buttress and the iliac tubercle start to appear later in juvenile australopithecines than in human children. This new feature on the australopithecine ilium modified fundamentally neither the pelvic growth pattern, which was ape-like, nor functional parameters during the growth as is the case in modern humans. On the other hand, evolutionary changes in the hominid growth pattern suggest significant change in bipedalism from *Australopithecus* to *Homo*. Not only does the pelvis become proportionally narrower, and the iliac blades become more sagittally positioned, but the hindlimbs also become proportionally longer. Recently, Steudel (1994) and Webb (1996) have discussed the evolutionary significance of the increased lower limb length in human evolution. They suggest that long hindlimbs provide no real advantage in terms of speed and energetic cost. However, long hindlimbs have to be connected with the change in pelvic morphology. Biomechanical studies of australopithecine bipedalism suggest marked differences in comparison with modern humans both in static and dynamic conditions. For example, the australopithecine morphology suggests that these forms moved with a

sort of waddling gait, involving large rotational movements of the pelvis and shoulders (Zihlman and Hunter, 1972; Berge, 1991b, 1994; Rak, 1991; Tardieu, 1991). Stern and Susman (1983) and Susman et al. (1984) demonstrated that the australopithecine postcranial morphology indicates an adaptation for movement in the trees. Berge (1994) also demonstrated that structural features differed from *Homo* in having less stabilization of the bipedal stance, and less ability for internal rotation of the pelvis and for extending the thigh in bipedalism. This makes it likely that modification of body proportions and body size corresponded to selective advantages for walking and running long distances.

Evolutionary interpretation in terms of heterochrony

When limited to multivariate morphometry, the present results lead to contradictory heterochronic interpretations. In Fig. 12, the changes in iliac proportions during growth in australopithecines (ancestral pattern) and humans (descendant pattern) are widely divergent: 1) fetal and neonate descendants fall with adult ancestors suggesting an acceleration (peramorphosis), whereas 2) adult descendants are situated with juvenile ancestors suggesting retardation (paedomorphosis). However, other results based on morphological observation and allometric calculation indicate clearly that the hypothesis of retardation has to be rejected. The similarity in iliac proportions in adult descendants and juvenile ancestors results from new morphological traits which reflect several accelerations, rather than the retention of ancestral juvenile traits. In other terms, the human ilium, and more specifically its anterior portion corresponding to the iliac plane, becomes proportionally narrower during growth because of its increasingly incurved nature with the displacement of the iliac buttress in a more dorsal position. Such accelerative processes superficially reflect paedomorphosis.

The change in pelvic shape and proportions observed during hominid evolution (from *Australopithecus* to *Homo*) resembles the change observed in human ontogeny (from neonate to adult). The main phenom-

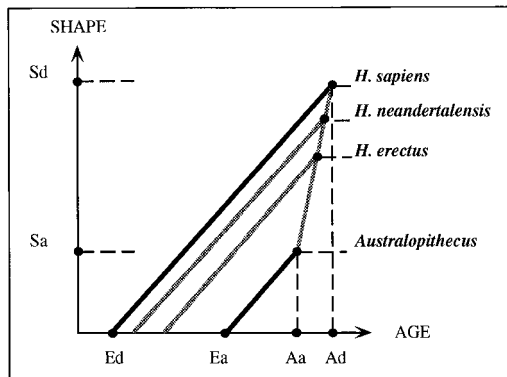


Fig. 14. Hypothetical heterochronic changes in hominid ontogeny. This representation is adapted from the methods of Alberch et al. (1979). The event (E), i.e. the formation of the acetabulo-cristal buttress on the ilium, appeared at the juvenile period in ancestral form represented by *Australopithecus africanus* (Ea); whereas it appears at the period of birth in present day descendants (Ed). The age of adulthood was attained earlier in ancestral form (Aa) than in human descendant (Ad). *H. erectus* and *H. neandertalensis* are intermediary forms between the ancestral form and the human descendant. Thus, the recapitulation is produced here by three heterochronic processes, that is to say by pre-displacement (Ea to Ed), hypermorphosis (Aa to Ad), and acceleration of shape changes (Sa to Sd).

enon in hominid evolution began with the appearance of a new morphological feature, that is the acetabulo-cristal buttress (or cristal tubercle on the iliac crest), which appeared probably with the practice of bipedalism in the first hominids. The present study suggests that the acetabulo-cristal buttress appeared progressively earlier in the life of descendants, until it arose at the time of birth in modern humans. Fig. 14 illustrates this hypothetical change in hominid ontogeny, that is to say a pre-displacement in time of the key element (acetabulo-cristal buttress), from the juvenile period of growth in ancestral form (Ea), to the time of birth in descendant (Ed). Apparently, a phenomenon of accelerated change in the pelvic morphology may occur in hominid evolution between these two stages. This peramorphic process should correspond to a change in ontogenetic allometries (from an ape-like iliac growth to a human-like one). This phenomenon is also suggested by the progressive change in adult iliac morphology, from *Australopithecus*, to *Homo erectus*, *H. neandertalensis* and *H. sapiens*. It is particu-

larly remarkable that the pelvic pattern of *Homo erectus* retained some australopithecine-like traits, and that these are still partly visible in *Homo neandertalensis*. Another heterochronic process is the prolonged growth at the end of the adolescent period, which reflects an evolutionary stage after *Australopithecus*. The ancestor (Fig. 14: Aa) ceased growth shortly after puberty, whereas the descendant (Ad) continued it. Such temporal hypermorphosis allowed the human descendants to have longer hindlimb segments and a greater body height than the hominid ancestors. It is probable that the process began with the first *Homo erectus*, which already had a human-like body size.

In conclusion, it now seems evident that heterochrony has played a central role in the evolution of the hominid morphology, not only for the skull but also for the post-cranium. The present study demonstrates clearly that the concept of neoteny is irrelevant for the pelvis. The study rather implies an accelerated evolutionary process than a retarded one. In a general manner, the results indicate that heterochronic processes may affect a single structure (for example, pre-displacement of the acetabulo-cristal buttress), an entire organ (accelerated change of the pelvic proportions), and again several post-cranial elements (covariation of pelvic and hindlimb change in length with time hypermorphosis). Whatever the diversity of combined processes in hominid evolution, it should be noted that the morphological changes of the skull and the post-cranium seem to be in opposite directions; there are paedomorphic changes of the skull, and peramorphic changes of the post-cranium.

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